Paleozoic vegetation increased fine sediment in fluvial and tidal channels: Evidence from secular changes to the mudrock content of ancient point bars

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ABSTRACT

The amount of mudrock preserved globally in alluvium increased in stratigraphic synchrony with the Paleozoic evolution of land plants. This observation has been explained by vegetation promoting both the retention of mud through baffling, stabilization, and flocculation, and the production of mud through chemical weathering. However, the latter explanation has been challenged on the basis that it is perceived to require imbalance in the long-term global carbon cycle. Here we present a compendium of empirical evidence that is supportive of increased global fine sediment supply and thus the contention that land plants did in fact promote the production of mud on the continents. We refine previous broad-brush analyses of Paleozoic mudrock content by specifically tracking shifts in the mudrock content of regions of alluvial and tidal landscapes that remained locally unvegetated even after the greening of the continents, namely inclined heterolithic stratification (IHS) that record submerged in-channel bars. We show that the Paleozoic mudrock increase was pronounced even within these areas,
away from any biomechanical binding and baffling effects of plants. Precambrian and Cambrian IHS are composed almost exclusively of sandstone, whereas Silurian through to Carboniferous examples show a steady increase in total mudrock content. This progressive rise in the mudrock component of channel bars cannot alone be explained by physical retention of mud by vegetation and requires heightened fine sediment concentrations from the hinterland, suggesting plants increased the volume of mud available at source. The muddying of Earth’s preserved IHS serves as a proxy that suggests evolving Paleozoic land plants triggered a global increase in the production and supply of fine-grained sediment.

LAND PLANTS AND MUD

Alluvial sedimentary strata deposited after the evolution of land plants contain a proportion of mudrock that is, on average, twenty times greater than equivalent strata from the preceding 90% of Earth history (Davies and Gibling, 2010a; McMahon and Davies, 2018; Fischer, 2018; Dahl and Arens, 2020; Brückner et al., 2021; Zeichner et al., 2021). Two categories of non-exclusive explanations have been proposed to account for this material stratigraphic shift, invoking the known influences of extant plant life on muddy sediment: 1) Plants increased total mud production on the continents through heightened silicate weathering (e.g., Knoll and James, 1987; Moulton et al., 2000; Quirk et al., 2012; Mitchell et al., 2016, 2019; Dahl and Arens, 2020); and 2) Plants promoted the retention of mud on the continents, preventing it from being bypassed out into the marine realm through below-ground stabilization of sediment (Dalrymple et al., 1985), above-ground baffling of fluids and sediment (Kleinhans et al., 2018), and the release of organic by-products that promoted flocculation and therefore deposition (Zeichner et al., 2021). Understanding the balance of mud production and retention is important because mud is integral to our comprehension of the ancient Earth system. The weathering of
clay minerals is an important function within the carbon cycle and any shifts in its intensity or
distribution would have had cumulative effects on the nature of global biogeochemical cycling
(Galvez et al., 2020). Mudrocks and their associated clay minerals are also significant archives
of ancient climate (Porada et al., 2016), ocean chemistry (Kalderon-Asael et al., 2021), and
fossil life (Anderson et al., 2021), and determining why and how their global volume fluctuates
can highlight potential biases in our understanding of the evolution of these phenomena.

Some model-driven arguments have suggested that the rise in alluvial mudrock must be
dominantly a result of physical retention; assuming that over long timescales the production of
mud through chemical weathering must be self-limiting because it is reliant on a finite supply
of CO$_2$ supplied by volcanic degassing (Fischer, 2018; D’Antonio et al., 2020; Zeichner et al.,
2021; Ielpi et al., 2022). However, other lines of evidence suggest that a Paleozoic increase in
continental mud production cannot be ruled out, even if that increase is balanced out elsewhere
by a counteracting carbon input (D’Antonio et al., 2020): pre-vegetation mudrocks have been
shown to be predominantly products of physical erosion rather than pedogenic clay mineral
formation (Rafiei and Kennedy, 2019; Rafiei et al., 2020), global geochemical data suggest
that the primary locus of the global ‘clay mineral factory’ shifted from the oceans to the land
in the early Paleozoic (Kalderon-Asael et al., 2021), and the isotopic signatures of zircon
formed at subduction zones show a marked shift coeval with vascular plant evolution, linked
to the greater mudrock content of subducting slabs (Spencer et al., 2022). Any empirical
evidence that the evolution of land plants did increase global chemical weathering products
necessitates a re-evaluation of our understanding as to how the global carbon cycle was
balanced in deep time.

The physical sedimentary record can yield clues as to whether physical retention was the sole
explanation for the Paleozoic mudrock surge. Mud retention in isolation would be restricted to
those environments where land plants were living and offering biomechanical binding and
baffling effects, or quiet water settings where volumes of flocculated mud could accumulate (Fig. 1). Thus retention alone could explain the abundance of later Paleozoic muddy floodplains (McMahon and Davies, 2018) but mud within more motile or submerged alluvial landscape elements would require an alternative explanation, as these would have been less hospitable to colonization by plants (especially the earliest, diminutive vegetation: Edwards et al., 2015). Modern analogues show that the mud content of fluvial channel bars is directly relatable to external fine sediment supply from upstream reaches, because barform topography creates locally variable flow conditions that capture fine-grained material to deposit if available (Szupiany et al., 2012). Increased fine sediment supply also heightens the propensity for flocculation and mud aggregation to occur, particularly in distal, tidally influenced channels where transported clay suspensions encounter saline waters (Seiphoori et al., 2021). The flux of mud through a system is thus a dominant control on in-channel volumes of deposited fine-grained sediment (Wysocki and Hajek, 2021), meaning the net quantity of mud observed to be preserved internally within channel barforms can act as a coarse proxy for the net volume of fine sediment supplied from upstream regions of mud production.

In this paper we refine previous, coarsely-resolved studies of alluvial mudrock abundance in the Paleozoic (McMahon and Davies, 2018) and specifically focus on the abundance of mud within sedimentary architectural elements that were deposited in submerged channel areas uncolonized by land plants. Since they have been commonly reported in published literature, we focus specifically on Precambrian to Paleozoic-age point bar deposits, which are most frequently revealed as inclined heterolithic stratification within alluvial strata (Fig. 2).

**INCLINED HETEROLITHIC STRATIFICATION**

Inclined heterolithic stratification (IHS) (sometimes referred to as ‘lateral accretion’ (LA), LA-IHS or epsilon cross-strata) is the alluvial architectural element that records point bar sedimentation (Thomas, 1987). The grain-size of sediments that form IHS can be highly
variable (Fig. 2) and Thomas (1987) referred to three broad classes: 1) dominantly homogenous, usually sand-grade or coarser material (also known simply as “inclined stratification” [Thomas, 1987]); 2) sand-grade or coarser IHS, with each set capped with a discontinuous fine-grained component; and 3) IHS with a continuous fine-grained component, either covering the entire sigmoidal surface or occurring within repeated coarse-to-fine grained couplets. In this study a fourth class is differentiated: 4) IHS composed of >50% mudrock. The term ‘mudrock’ is applied as an umbrella term incorporating multiple types of fine-grained sediment (< 62.5 μm grains: mudstone, siltstone, claystone). While ancient examples of IHS are frequently reported (Table S1), few instances have been explicitly grouped into these classes. To interrogate long-term trends, we here classify examples from 92 previously described Proterozoic to Carboniferous instances of IHS from ancient channels, through reference to published descriptions or images, in addition to original field investigations of 44 of these instances (Table S1). All the original channels would have had variable mudrock content (and therefore IHS classes) along and across strike and they have been randomly sampled as natural outcrops that record only a spatial fraction of their primary form (e.g., Davies et al., 2019). Our analysis of the IHS record encapsulates the entire collection of the random samples that have been preserved, thus providing an empirical account of stratigraphic shifts in IHS class abundance that, through its inclusivity, over-rides the imperfection of individual records. To identify whether IHS were tidal or fluvial, we followed published interpretations in instances where we did not ground-truth the successions, but note the caveat (after Thomas, 1987) that some ancient tidal IHS may have been misinterpreted to be fluvial, particularly as tidal currents can propagate landward through meandering channels for several kilometres with only cryptic sedimentary signatures (Ghinassi et al., 2021).

**PROTEROZOIC – PALEOZOIC EVOLUTION OF POINT BAR SEDIMENTATION**
Our data shows that tidal IHS increased in abundance through the Paleozoic; a trend also previously reported for fluvial IHS (Davies and Gibling 2010b) (Fig. 3). Within this overall trend, mudrock-rich IHS components become particularly prominent. Mudrock is a minimal component of both tidal and fluvial IHS in the Precambrian-Ordovician but becomes a common or dominant lithology from the Silurian onwards. Class 1 IHS account for 75% of Precambrian to Ordovician examples (n = 18). In the Silurian this value drops to 7% (n = 9) and remains under 33% for each subsequent studied interval (n = 89). Class 3 IHS form an increasingly large percentage of the total number through the Silurian (27%), Devonian (34%) and Carboniferous (35%) (n = 9, 35, 54 respectively). The earliest class 4 IHS occur in the Silurian and account for 10% of Silurian to Carboniferous examples (n = 98). Both fluvial and tidally influenced IHS display comparable IHS muddying through the Paleozoic (Fig. 4), though class 1 IHS are more common in purely fluvial examples (36% vs 19% of total number (n = 74 and n = 48, respectively)).

**DISCUSSION**

Paleozoic trends in the abundance and character of IHS demonstrate that not only did meso-scale point bars become more commonly interred in the stratigraphic record, but also that the amount of mud that was trapped in these landforms, in both their emergent and submerged flanks, increased synchronously with the global increase in net alluvial mudrock (McMahon and Davies, 2018) and the advent of widespread land plants (Wellman et al., 2022). Significantly, pervasive muddying occurs across submerged and flowing water parts of both fluvial and tidal channels (Fig. 3, 4). Such instances cannot be accounted for by a universal explanation of global mud retention by land plants because they are located away from *in situ* vegetation that could promote physical retention, and quiet water settings where volumes of flocculated mud could accrue. The incorporation of mud into IHS fundamentally requires sufficient clay suspensions (Wysocki and Hajek, 2021), regardless of whether its deposition is
forced through tidal influence (Johnson and Dashtgard, 2014), varying fluvial discharge (Bridge and Jarvis, 1976), scroll bar passage (van de Lageweg et al., 2014), local topography (Szupiany et al., 2012) or the mixing of riverine and saline waters (Seiphoori et al., 2021). An overall trend towards muddier IHS (Fig. 3, 4) thus implies increased availability of clay-grade sediment from the Silurian onward and incorporates a number of source-to-sink conduit environments, in both their submerged and emergent reaches, and irrespective of locations where vegetation would have been growing. Such an increase is implicit of increased mud availability from the hinterland, presumably both directly weathered from bedrock in the source area, and recycled from and neoformed within increasingly stable staging areas such as floodplains, where liberated sediment could undergo multiple further rounds of weathering. Increased fine sediment supply would also promote greater aggregation of clay into flocs (Lamb et al., 2020; Wysocki and Hajek, 2021), a mechanism which, in conjunction with the rise in terrestrial organics associated with early plants (Zeichner et al., 2021), would enhance mud settling and deposition on out-of-channel floodplains. A positive feedback loop therefore exists between mud production and mud retention through flocculation.

The progressive Paleozoic muddying of both preserved IHS and total alluvium (McMahon and Davies, 2018) supports the contention that the evolution of land plants increased both mud production and retention on the continents. Whilst the relative contributions of mud production versus mud retention remains unknown, this geological evidence for heightened mud production by early plants fits our understanding of the integral roles played by modern land plants in chemical weathering (e.g., by promoting chelation, hydrological connectivity between atmosphere and lithosphere, and the depth of CO₂ diffusion in substrates) (e.g., Berner, 1992; Moulton et al., 2000; Quirk et al., 2012). The empirical evidence for increasing mud production is in apparent conflict with mass-balance models of the long-term carbon cycle (e.g., D’Antonio et al., 2020; Ielpi et al., 2022), highlighting that a similar census of mudrock
distribution in Precambrian and Paleozoic marine environments, which will provide insights
into the universal distribution of mud on ancient Earth, is overdue.

CONCLUSION

The fine-grained component of inclined heterolithic stratification (IHS) increases in abundance
through the Paleozoic. Whereas instances of IHS in the Precambrian and Cambrian are
dominantly composed of sandstone, from the Silurian onwards they are more frequently
organized into distinct sandstone-mudrock couplets or mudrock-dominant IHS. This
progressive rise in the fine-grained component of IHS is synchronous with the rise of terrestrial
vegetation, which has previously been implicated in the concomitant rise in bulk alluvial
mudrock, attributed to both the production and retention of mud by plants. Significantly, the
mudrock shift occurs across both fluvial and tidal environments, requiring that the volume of
fine-grained sediment in these conduits increased, and cannot be explained solely by the
physical retention of fines by land plants as biomechanical agents. This empirical observation
strongly supports hypotheses that the Paleozoic expansion of land plants not only acted to stop
mud from leaving the continents but also reorganized the carbon cycle by enabling new
pathways in chemical weathering, mud production, and source-to-sink sediment fluxes.

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Figure 1. Mechanisms suggested to account for the shift in alluvial mudrock coeval with the evolution of plants. Flocculation: Following the onset of vegetation plant organics promoted aggregation of clay into flocs in rivers and facilitated mud deposition on floodplains (Zeichner et al., 2021). Binding: SEM image depicts moss (Racomitrium sp.) rhizoids binding soil. The fastening of masses of grains by plant parts such as roots mechanically strengthened channel banks, increasing the likelihood of out-of-channel mud retention (Davies and Gibling, 2010a). Baffling: SEM image of moss baffling sediment. Above-ground plant parts trapped grains (white arrows), with the greater abundance of deposited muds elevating local floodplain topographies and reducing the strength of overbank flows (Kleinhans et al., 2018). Increased abundance of inclined heterolithic stratification deposited by meandering channels following the expansion of vegetation reflects previous assessments of the rock record (Davies and Gibling, 2010b).
Figure 2. Inclined heterolthic stratification (IHS): A) Class 1 IHS from the Visean Largysillagh Formation, Ireland; B) Class 2 IHS from the Pragian Traeth Lligwy Beds, Wales C) Class 3 IHS from the Visean Shalwy Formation, Ireland; D) Class 4 IHS from the Emsian Black Nore Sandstone Formation, England.

Figure 3. Top: Reported IHS by age and environment. Middle: Reported IHS by type per million years. Bottom: Percentage of total number of IHS reported from the Paleoproterozoic to end Carboniferous.

Figure 4. Percentage of fluvial (top) and tidally influenced (bottom) IHS reported from the Paleoproterozoic to end Carboniferous.

Supplementary Material. A) Methodology followed for database construction and analysis. B) Table S1. Reports of inclined heterolithic stratification (IHS). Please visit https://doi.org/10/1130/XXXX to access the supplementary material, and contact editing@geosociety.org with any questions.
Figure 2

Class 1: Homogenous sand or coarser

Class 2: Sand-grade or coarser with discontinuous fine-grained drapes

Class 3: Distinct coarse-to-fine grained couplets

Class 4: Mud dominated